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NATURAL HISTORY AND ACOUSTIC REPERTOIRE OF THELARGE-FOOTED FINCH (*PEZOPETES CAPITALIS*), AN ENDEMIC, HIGHLAND BIRD OF COSTA RICA AND WESTERN PANAMA

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Resumen. – Historia natural y repertorio acústico del Sancuinclas (*Pezopetes capitalis)*, ave endémica de Costa Rica y el oeste de Panamá. – El Sancuinclas es una especie endémica y un habitante común del sotobosque de bosques montanos y páramo en las tierras altas de Costa Rica y el oeste de Panamá. A pesar de ser una especie común, existía poca información sobre su biología reproductiva e historia natural. En este estudio describimos aspectos de su uso del hábitat, comportamiento reproductivo, cuido parental y su repertorio acústico. Las parejas de esta especie son monógamas y territoriales, y cada una de ellas se reproduce más de una vez por año, sin embargo, la reproducción es asincrónica entre las parejas. Ambos sexos participan en la construcción del nido y el cuido de su descendencia (usualmente un polluelo en cada evento reproductivo). El repertorio acústico del Sancuinclas consiste de dos cantos, los cuales difieren en sus características acústicas y temporales (e.g., rango de frecuencia, frecuencia alta y baja). El primer canto es un solo, el cual lo canta el macho en dos contextos: cantos mañaneros y despliegues territoriales agresivos. El segundo canto es un dueto altamente sincronizado, cantado por ambos sexos, sin embargo, algunas veces los machos cantan de manera solitaria su parte de los duetos. Los duetos son cantados cuando una pareja se reúne luego de una separación espacial, o de manera más frecuente cuando se dan despliegues territoriales defensivos.

Abstract. – The Large-footed Finch is a common, endemic inhabitant of the understory of montane forest and páramo in the highlands of Costa Rica and western Panama. Although this species is common, information regarding its reproductive biology and natural history is scarce. In this study, we described habitat use, reproductive behavior, parental care, and the acoustic repertoire of the Large-footed Finch. Pairs are monogamous and territorial, and each pair reproduces more than once a year, but reproduction among pairs is asynchronous. Both sexes participate in nest construction and offspring care (usually one chick per breeding event). The acoustic repertoire of the Large-footed Finch consists of two song types, which differ in temporal and acoustical characteristics (e.g., frequency range, maximum and minimum frequency). The first song is a solo used by males in two contexts: morning songs and territorial aggressive displays. The second song is a highly synchronize duet, sung by both sexes, though sometimes the male sings its part of the duet alone. The duet is sung when a pair reunites after a spatial separation, or more frequently as a territorial defensive display. *Accepted 4 September 2014.*

Key words: Large-footed Finch, habitat use, biparental care, acoustic repertoire, duet, territory defense.

INTRODUCTION

The Costa Rican avifauna is characterized by a high diversity of highland endemic species (Slud 1964, Stiles & Skutch 1989, Hernández-Baños *et al.* 1995). The assemblage of this endemic avifauna has been the result of both historical and ecological factors (Drake 1991,

Barrantes 2009). A series of complex geological and climatic events, including the formation of the cordilleras, and cold climatic conditions during the upper Pleistocene, promoted dispersal of bird species from the Neartic region and from Andean highlands (Nylander *et al.* 2008). Periods of inter-glacial conditions reduced the connectivity between these regions, isolating populations of the species established in the highlands of Central America from their ancestral populations, and promoting subsequent speciation (Hackett 1995, Pérez-Emán 2005, Barrantes 2009).

The highland avifauna of Costa Rica and western Panama includes 85 resident species (Barrantes 2009), 34 of which are endemic to these highlands. The composition of this avifauna was first described by Slud (1964) and a series of subsequent papers described general aspects of their natural history (Wolf 1969, Colwell *et al.* 1974, Naoki 1998, Wilms & Kappelle 2006, Barrantes 2009, Barrantes *et al.* 2011), morphological and genetic divergence (Stiles 1985, Barrantes & Sánchez 2000, Chavarría *et al.* 2010), and feeding and behavioral aspects of some species, particularly hummingbirds (Wolf *et al.* 1976, Stiles & Freeman 1993, Fuchs *et al.* 2010, Ávalos *et al.* 2012). However, despite the uniqueness of this diverse, endemic avifauna and the interest in preserving this entire ecosystem (Kappelle 2006, Sánchez & Barrantes 2011), detailed information on the natural history and reproductive biology is available for only a few species (Hunt 1971, Barrantes & Loiselle 2002).

The Large-footed Finch is a common endemic species of Costa Rica and western Panama. In Costa Rica, it inhabits the understory of montane forest and páramo in the Central and Talamanca Cordilleras (Slud 1964, Stiles & Skutch 1989). There, this species is a ground-dwelling finch which forages in small, open areas covered with a thick layer of leaf litter within dense forests and bamboo thickets (Wolf 1976, Stiles & Skutch 1989). It breeds in dense forest undergrowth, forest clearings and forest edges; its nest is a massive cup made of seed-stalks and bamboo leaves, and is constructed within dense-foliage bushes or clumps of bamboo stems at ca. 1.5 to 2 m above the ground (Klein *et al.* 1991). The clutch consists of one elliptical or sub elliptical shaped egg (Stiles & Skutch 1989, Klein *et al.* 1991). Other information on the reproductive biology and natural history of this species is largely unknown. In this study, we describe habitat use, reproductive behavior, parental care, and the acoustic repertoire of the Large-footed Finch.

METHODS

Study population. We conducted this study at the Estación Biológica Cerro de la Muerte (09º34'N, 83º41'W; 3150 m a.s.l.) from April 2009 to May 2009, and March 2011 to December 2012. Most of the study area is covered by an old second growth oak-forest (*Quercus costaricensis*), with its understory dominated by dense thickets of bamboo (*Chusquea* spp.) (Stiles & Skutch 1989), and some bushes and treelets of the families Ericaceae and Melastomataceae.

Natural history. We identified the territory of 15 mated pairs. We followed each mated pair from one to 15 non-consecutive days, marking foraging area and movement routes with flagging tape. We did not measure the area of territories but we used this information to set the mist-nets and band both individuals from five pairs, and one individual from other five pairs. Each individual had a unique combination of colors. We identified the other five pairs based on their presence in limited areas and previous observations of territory fidelity in this species. Descriptions of territories, foraging behavior, reproductive behavior, and parental care are based on direct observations

and video recordings of some pairs made with a digital video camera (Sony HDR-SR11) in the field.

For each pair we classified observations in two categories: a) Non reproductive period: when birds were engaged only in foraging activities, without indication of courtship or nest construction behavior. b) Reproductive period: when one or both members in a pair engage in nest construction (carrying nest material), members of the pair foraged alone (this is expected to occur when the other bird was attending the nest), and caring for offspring. Based on our field observations, we divided young in three qualitative age categories: 1) Chick: a fledgling outside its nest, with yellow bill, strongly barred chest, and tail no longer than 3 cm. 2) Pre-juvenile: an individual with yellow bill, barred chest, tail as long as that of an adult, and green head with black stripes. 3) Juvenile: an individual with black bill, barely barred chest, tail as long as that of an adult, head with the same color pattern as an adult, and iris brownish rather than reddish (adult iris color). Juveniles foraged actively with their parents.

Song repertoire. We recorded solo songs from five birds and duet songs from 12 pairs. In cases where an individual or a mated pair did not sing, we used playbacks from other individuals to induce a response. We held the microphone at 1 m above the ground and at a distance of 5 m to 10 m away from the focal individual during recordings. We used two playbacks (LCH 12-001 and LCH 12-003) from birds recorded in Barva National Park (74 km away from the study site), obtained from the Bioacustic Lab, University of Costa Rica; the third playback was from a bird recorded in 2009 at the study site.

For all recordings we used a directional microphone (Sennheiser ME66) and a solid state digital recorder (Marantz PMD 620, from April to May 2009; Marantz PMD 661, from March 2011 to December 2012). We saved digital recordings as uncompressed monoaural WAV files (24-bit and 48-bit, 44 kHz) and analyzed them using Raven pro 1.4. (Bioacoustics Research Program 2011), with the following settings: a temporal resolution of 5.3 ms, frequency resolution of 270 Hz in a Hann window with 188 Hz sampling and 50% overlap.

For the identification of the elements that corresponded to each individual in a duetting pair, we used two approaches. 1) We recorded videos in HD definition using a Sony HDR-SR11, for three mated pairs (two banded pairs and one unbanded) in which we knew beforehand the sex of each individual (based on behavior during duetting and foraging, and morphometric measures; unpublished data), allowing us to determine their duetting order. We identified sex of birds based on presence of brood patch and cloacal protuberance; none of the birds with cloacal protuberance had brood patch suggesting that only females incubate eggs (GB unpublished data). In addition, the wing cord and tail length (mean ± sd in mm) of males are larger than those of females (wing: males 90.85 ± 2.52, females 83.55 ± 3.05; tail: males 88.10 ± 4.07, females 81.64 ± 2.97; n = 13 and 11, respectively). 2) In playbacks trials, we directed the microphone to one individual as it was responding. We identified each bird recorded based on its band color, or in the band color of its partner, in those pairs in which we banded only one individual of the pair. In all cases in which at least one bird in the pair was banded, the acoustical signal of the focal individual (in front of the microphone) displayed a darker tone on the spectrograms. This condition helped us to define the identity of those birds recorded from pairs in which none of the members were banded. We defined an element as a discrete sound represented in the spectrogram that can be separated temporally or in frequency from other elements.

RESULTS AND DISCUSSION

Habitat use and abundance. We observed pairs foraging together all year round in the understory of montane oak forest, second growth forests, *Chusquea* spp. tickets, and open areas with disperse Ericaceae and Rosaceae bushes. Large-footed Finch individuals foraged from dawn to dusk. The activity initiated with males singing solo songs from dense thickets, and they continue singing intermittently for periods of 10 to 20 min, until foraging activity began. The birds foraged in pairs, scratching the leaf litter, and occasionally going up in a bush, looking for small (unidentified) insects and occasionally some berries (e.g., *Rubus* sp.). Wolf (1976) also reported insects, seeds, and fruits, especially of *Pernettya*, as the main food items for this species.

The same pairs (banded birds) foraged actively in the same area for more than one year. They foraged, roosted and bred within their territories; in two of the territories the pair collected material for nest construction (also noted by Klein *et al.* 1991). Mated pairs attacked conspecifics when they invaded their territories, and also responded intensely, both physically (e.g., constant movements between brushes) and acoustically, when we used playbacks stimuli to simulate territory intrusion. We counted 19 pairs in a 50 ha area, but some pairs may have gone undetected; according to F. G. Stiles (pers. comm.) the estimated size of territories for the Large-footed Finch is ca. 1 ha. When a pair perceived an intrusion of conspecifics (or playback recordings) in their territory, the male first approached to the source of the song, followed shortly by the female, then both sang a sequence of duets (from 1 to 4). If the male approached the playback source alone, he usually sang a sequence of solo songs that lasted as long as 5 min as he moved between branches.

Within their territories, Large-footed Finch individuals seemed to follow particular foraging routes each day. We recorded this pattern in six pairs, in which we saw them foraging on the same area almost at the same time for several days (3 to 10 days). The foraging areas often overlapped with adjacent territories (n = 8 of 15 territories), but birds did not enter far into neighboring territories, and did not enter at all when the other pair was present. The same behavior was described by Wolf (1976), who stated that pairs seemed to restrict their activities to one area at a given time, but foraging areas of some pairs often overlapped.

Reproductive behavior and parental care. Half of the pairs (n = 5 of the 10 pairs banded) remained together for at least 18 months. From these pairs we registered two divorces. In one case, the male paired with a new mate and raised a chick five months later, close to his former territory. For the second pair, we observed the female with a new mate six months later and the male with a new mate and a chick eight months after the divorce. In this particular case, the female maintained the same territory she had prior to divorce, while the male was seen foraging in an adjacent territory. Though divorce is relatively common in birds (McNamara & Forslund 1996), the reasons for divorce in monogamous birds are still poorly understood. It is thought that at least for one of the mates in a pair the fitness increases by divorcing and remating with a higher quality mate (Choudhury 1995, Otter & Ratcliffe 1996), but only long-term studies combined with studies of paternity will provide information on fitness of divorced individuals.

Reproduction was asynchronous across pairs, and occurred nearly throughout the entire year. We registered pairs with young from February through September (Fig 1.); breeding apparently decreases from October to February, the driest period of the year. Some pairs had multiple reproductive events

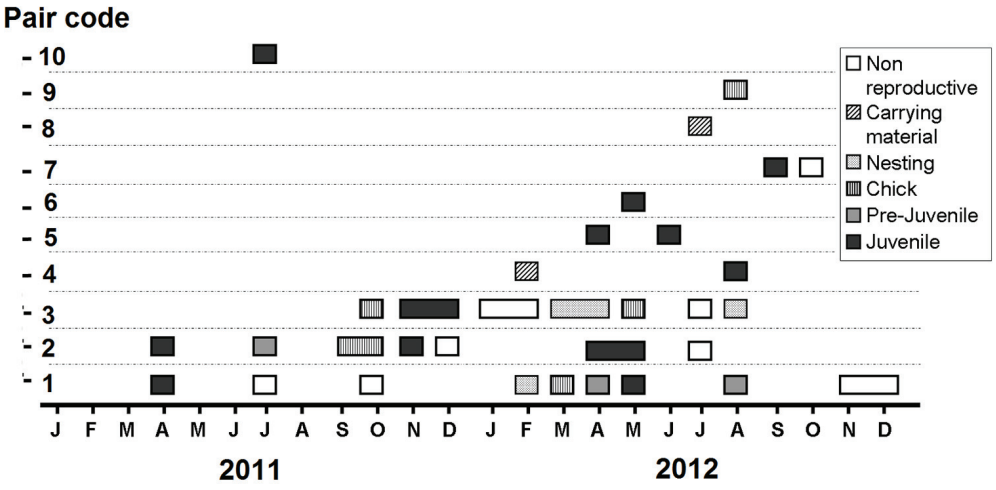

FIG. 1. Period of reproductive and non-reproductive events by pairs of the Large-footed Finch, Cerro de la Muerte, Costa Rica.

in a year. One pair had three breeding events in one year, raising one chick each time, approximately three months apart from each other. Nearly always a pair raised a single chick (14 out of 15 pairs), but one pair raised two chicks on one occasion. The reproductive strategy of the Large-footed Finch is highly unusual even for tropical birds whose breeding season tend to be longer than that of temperate species (Martin 1996). Practically all tropical birds synchronize their breeding seasons to the availability of food critical resources (Stiles 1983). For instance, most insectivores tend to breed early in the rainy season when abundance of insects increases (Wolda 1982, Stiles 1983, Sandoval & Barrantes 2009). Hence, the extensive breeding season and small clutch size of the Large-footed Finch suggest the absence of a peak in food resources (e.g., ground dwelling insects), but this is yet to be tested.

Reproduction began with construction of the nest, which was described by Klein *et al.* (1991) as a massive cup built with bamboo (*Chusquea* sp.) leaves, grasses, mosses, stems, and twigs. They mentioned that in eight of nine nests the clutch consisted of a single egg. Chicks remained with their parents approximately three months (Fig. 1: see pairs 2, 3, and 5). To estimate this time, we counted the time from the first time we saw a chick with its parents until the juvenile abandoned (or was expelled) the parents' territory. For three pairs the period between the initiation of nesting events (carrying material) and the bird abandoning the parent's territory was at least five months (Fig. 1: see pair 3).

Both parents fed the chicks. Both chicks and pre-juveniles produced a low intensity begging call (*peep peep*) as their parents foraged nearby. Every time we heard a chick begging (n = 6), both parents proceeded to feed their offspring immediately. All three young stages (chicks, pre-juveniles, and juveniles) scratched the litter as adult do, but only pre-juveniles and juveniles captured prey occasionally. While foraging, all family members remained less than 5 m apart. When we approached a family (about 5 m away), the male approached us and then perched on a branch or stem at about 1.5 m above ground, while the female continued foraging with their offspring (n = 6

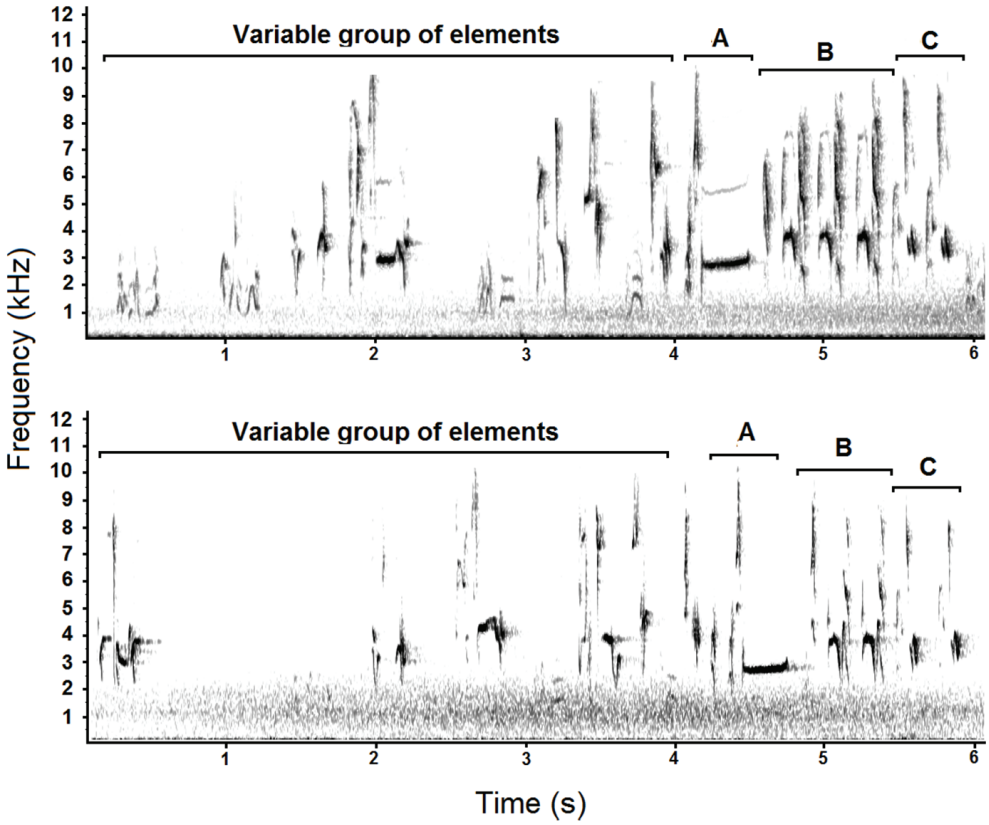

FIG. 2. Sound spectrograms depicting two solo songs (species song) produced only by males of the Large-footed Finch, Cerro de la Muerte, Costa Rica. The first part of a solo song, varies across males, and consists of different elements. A, B, C is a sequence of elements by all males in the same order.

pairs). Another response of the parents toward our intrusion was to hop away with their offspring, and hide their chicks or juveniles in dense vegetation, where the chick or juvenile remained very quiet and silent, and both parents returned immediately to foraging.

Our results show that Large-footed Finches have a strong biparental investment in parental care. The low environmental temperature prevailing in the highlands inhabited by the Large-footed Finch has likely promoted the evolution of both the high biparental investment and the extremely small clutch size in this species. Such small clutch size may be compensated by the capability of this bird species to reproduce up to three times a year.

Acoustic repertoire. Large-footed finches produced three different vocalizations year round: 1) a solo song ("species song" hereafter) sung only by males (Fig. 2); 2) duets which consisted of a sequence of antiphonal, highly coordinated elements produced by both males and females with a stereotyped acoustic pattern (Farabaugh 1982, Langmore 1998) (Fig. 3); and 3) a solo song produced by

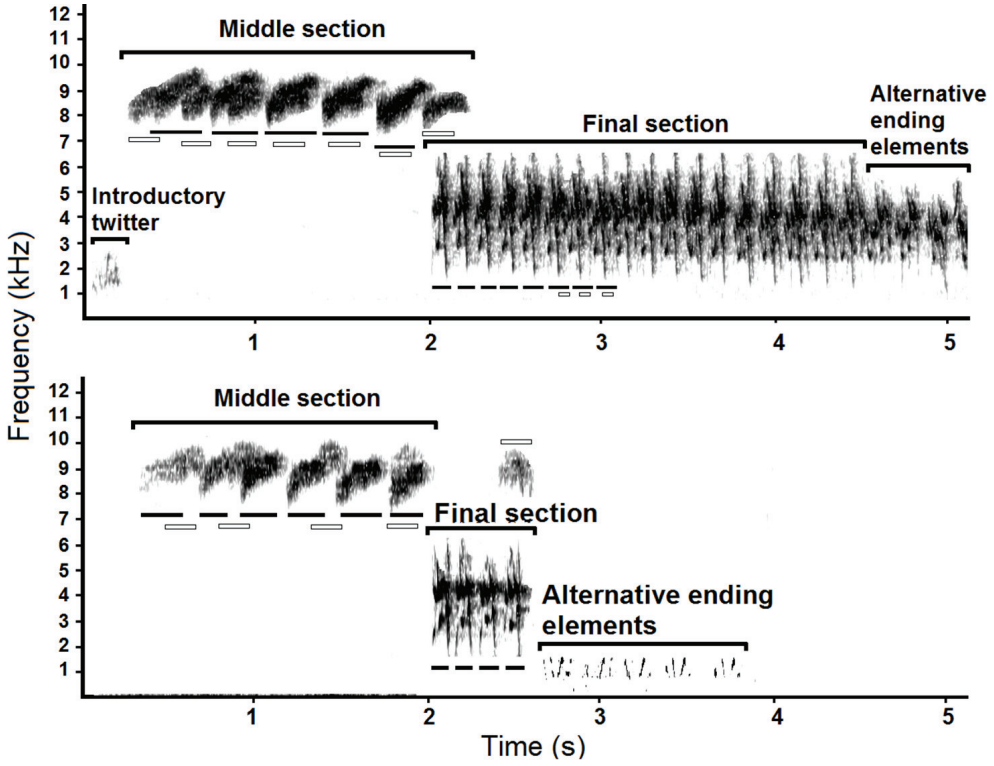

FIG. 3. Sound spectrograms of duets of the Large-footed Finch, Cerro de la Muerte, Costa Rica. Duets consist of 1) introductory twitter elements: can be sung by both sexes but are not present in all duets. 2) Middle section: group of overlapping elements that can be initiated by either the male or the female. 3) Final section: formed by a group of repeated and alternated elements between both members of a mated pair. (d) Variable group of elements which are not present in all duets. Spectrograms show elements sung by "individual 1" (black bars) and elements by "individual 2" (white bars).

males that consisted of the same elements used by the male in a duet (Fig. 4). We defined a song as a string of stereotyped elements separated temporally for at least one second from a similar string produced by males or females.

The song of the Large-footed Finch consisted of 10 to 18 elements, some of which were repeated, especially at the end of the song (Fig. 2). The beginning of the song was variable across males (n = 5), but the final part was very similar in all males (Fig 2: groups of elements A to C). This song differed in length and in the acoustical structure of elements among males (Table 1; we measured only those elements that were present in all males' songs).

The entire duet was divided into four sections (Figs 3a–d), which varied in length, and frequency (Table 1), but only the middle and final sections were present in all duets (n = 68). During the duet, the elements produced by both sexes overlapped in time and/or frequency along most of this vocalization. The introductory section of the duet consisted of a twitter-like sound that can be presumably sung by either sex. The bird that sang this first section was not the same that initiated the

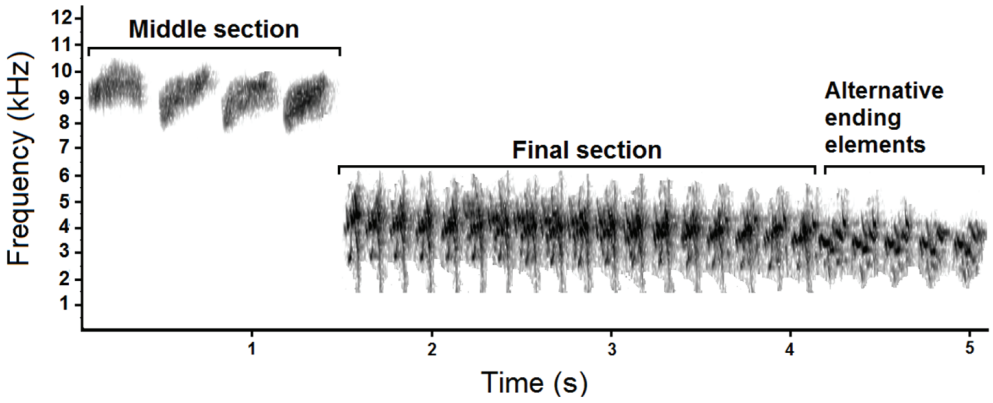

FIG. 4. Solo song of an individual of the Large-footed Finch, Cerro de la Muerte, Costa Rica. This song shares the same structure and elements of the duets, but is sung only by males.

middle section, because both sections overlapped temporally. This introductory twitter section was either absent in most duets, or had very low amplitude to be detected in the spectrograms (Fortune *et al.* 2011), so for the analyses we considered the middle section as the initial part of the duet of the Large-footed Finch.

The middle section consisted of a group of alternate overlapping elements sung by both members of a pair. The number of elements per individual in this section was 5 ± 1.4 (range: 2 to 9 elements). The final section consisted of 10 ± 4.6 elements (range: 1 to 21 elements) sung by each sex in alternate fashion, and most duets ended with this section, but some duets (n = 10 of 45 duets) had an additional section of 6 ± 2.8 (range: 2 to 10 elements) elements (Fig. 3d). We did not measure frequency (Hz) or duration of the elements of this section because we were unable to determine which sex sang this section in the duet.

The duet was produced in two different contexts. The first was when a pair perceived an intrusion of conspecifics (e.g., a playback) in their territory, and the second when the members reunite (seen only twice) after having being some distance apart (e.g., more than 10 m apart). The only function of the duet proposed for the Large-footed Finch was mate recognition (Wolf 1976, Stiles & Skutch 1989). However, the duet in this species likely serves multiple functions (e.g., territory defense, mate recognition and contact maintenance) as suggested by Hall (2009). On five occasions, we recorded a male singing alone its section of the duet in response to a playback.

Description of the reproductive biology, song repertoire and some general aspects of natural history of the Large-footed Finch are important to design future conservation policies not only for this species but for the rich endemic avifauna of Costa Rican highlands. In addition, the characteristics of vocalizations and breeding behavior of this species will help to elucidate the relationship of the Large-footed Finch between the two most related genera (Cadena *et al.* 2007, Cadena & Cuervo 2010, Klicka *et al.* 2014).

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TABLE 1. Acoustic parameters of the vocalizations of the Large-footed Finch, Cerro de la Muerte, Costa Rica: species song (n = 5 males) and duet song (n = 12 pairs)

Song type	Time (s)	High frequency (Hz)	Low frequency (Hz)
Species song			
A	0.34 ± 0.11	9920 ± 125	1439 ± 489
B	0.19 ± 0.05	10357 ± 1136	1710 ± 899
C	0.21 ± 0.02	9376 ± 594	1801 ± 222
Duet			
Introductory twitter	0.61 ± 0.22	2766 ± 469	552 ± 136
Middle section	1.98 ± 0.31	10100 ± 210	7238 ± 219
Final section	2.46 ± 0.54	5732 ± 299	1050 ± 320

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